BOULDER SUMMER SCHOOL 2011: INTRODUCTION TO LOW REYNOLDS NUMBER LOCOMOTION (NOTES FROM PEKO HOSOI'S LECTURE)

0.1 Reynolds Numbers in Biology

The Reynolds number is dimensionless group that characterizes the ratio of inertial to viscous forces. It is defined as

$$Re = \frac{\rho U L}{\mu} = \frac{UL}{\nu}$$

where ρ is the density of the medium the organism is moving through; μ is the dynamic viscosity of the medium; ν is the kinematic viscosity; U is a characteristic velocity of the organism; and L is a characteristic length scale. When we discuss swimming *biological* organisms, we are usually referring to creatures that are moving through water (or through a fluid with material properties very close to those of water). This means that the material properties μ and ρ are fixed[1] and the Reynolds number is roughly determined by the *size* of the organism.

In general, the characteristic size of the organism and the characteristic swimming velocity are related. As a rule-of-thumb, the characteristic locomotion velocity, U, in biological organisms is related to L by $U \sim L$/second e.g. for people $L \sim 1$ m and we move at $U \sim 1$ m/s; bugs are about $L \sim 1$ mm, and they move at about $U \sim 1$ mm/s; for microorganisms $L \sim 100$ μm and $U \sim 100$ μm/s. Obviously this is a very very very very rough estimate and one does not have to think very hard to come up with exceptions (as is always the case in biology!). However, it serves as a good starting point to estimate the Reynolds numbers for various biological organisms as illustrated in the sketch in Figure **??**. Note that even for organisms as small as ants, the Reynolds number is still on the order of 1 (which is not very low). In this lecture we will focus on $Re \ll 1$ which is relevant for single-cell organisms and bacteria.

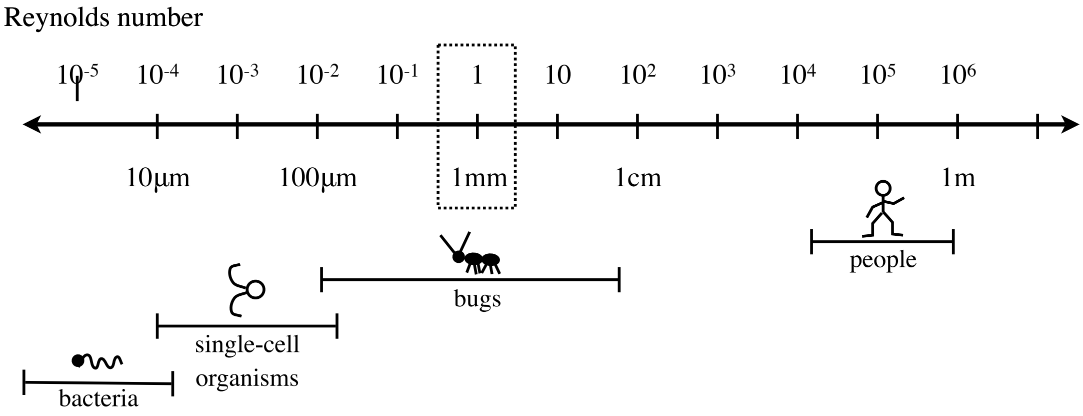

Figure 1: Typical Reynolds numbers for various biological organisms. Reynolds numbers are estimated using the length scales indicated, the "rule-of-thumb" in the text, and material properties of water.

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[1] For water, $\nu \approx 10^{-2}$cm^2/s and $\rho \approx 1$ g/cm^3.

At this point is is worth mentioning a few biological details about single-celled organisms. A good place to start is the well-known image sketched by fluid dynamist, James Lighthill (made in the days before PowerPoint). I haven't included the image here for fear of copyright infringement, but it is worth looking up and readily available in:

Reference: James Lighthill, "Flagellar hydrodynamics." *SIAM Review.* **18** (1976).

Lighthill's figure represents a fluid dynamicist's view of biology as he has classified the organisms first and foremost, not by any biological metric, but by how they swim. Organisms within the central circle all consist of a head (which is generally modeled as a sphere) propelled by N tails where N is a small number (generally 1, 2, or 3). Organisms outside the circle use some other mechanism or don't locomote at all.

On top of this division, there is a second (more traditional) biological classification. The semi-circle dividing the top of the image from the bottom, marks the dividing line between eukaryotic cells and prokaryotic cells. Roughly speaking, prokaryotic cells are bacteria and eukaryotic cells are everything else (people, fungi, grasshoppers, elephants, algae ...). This distinction between eukaryotic and prokaryotic swimmers is quite important because the structure of the tails (which determines the mechanics of swimming) is different in the two groups. For eukaryotes, the tail is made of flagellin and has a characteristic 9+2 microtubule structure. This has two important consequences:

1. By sliding the microtubules relative to one another, the organisms can exert a local bending moment anywhere along the length of the tail which means that the eukaryotic organisms can *select the shape of the tail as a function of time* (i.e. they can control the kinematics). This is in contrast to prokaryotic organisms which have a single motor that connects the tail to the head and hence can only apply a localized torque at the base of the tail.

2. Since all eukaryotic tails all have the same 9+2 microtubule structure, they all have roughly the same cross-sectional diameter. The length of the tail may vary from organism to organism, but the diameter is approximately 250–400 nm for all species (this includes cilia in our lungs, tails of green algae, tails of spermatozoa, etc.).

These differences between prokaryotic and eukaryotic tails and summarized in the following table:

Structure of Tails

Eukaryotes	**Prokaryotes**
flagellin	tubullin
distributed torque	concentrated torque
9+2 microtubule structure	
diameter of tail $\sim$ 300 nm	

0.2 The Physics of Low Re Swimming

At this point we need to introduce our next reference:

Reference: Purcell "Life at low Reynolds number" Scientific American (1977).

This is one of the most well-known papers on swimming at low Reynolds numbers and I highly recommend it for someone who is looking for a gentle introduction to the topic. For the purposes of this lecture, we will define swimming as follows:

Swimming: To undergo cyclic deformations that result in a net translation or/and rotation (with no externally applied forces or torques).

The governing equations for low Reynolds number flow around an organism undergoing such deformations are the Stokes equations:

$$\nabla p = \mu \nabla^2 \mathbf{u} \quad \nabla \cdot \mathbf{u} = 0.$$

In addition, the forces and torques on the organism must balance (since we are considering an inertialess world, there is no acceleration hence $m\mathbf{a} = 0$):

$$\mathbf{F} = \mathbf{0}, \;\; \mathbf{M} = \mathbf{0}.$$

A few features of swimming at low Reynolds number are readily apparent from these equations:

1. Usually when we balance forces in locomotions studies, we balance some propulsive force against drag (e.g. vortex shedding, inertia, etc.). However, at low Reynolds numbers the only thing that can balance drag is ... drag! Hence propulsion comes from the *anisotropy* in the drag force. At low Reynolds numbers the drag force on an object moving through a fluid is linearly proportional to the velocity: $\mathbf{F} \propto \mathbf{U}$ or

   $$F_{\perp} = C_{D\perp} u_{\perp} \qquad\qquad F_{\|} = C_{D\|} u_{\|}$$

   where subscripts indicate directions parallel to and perpendicular to the surface of the object (as shown in Figure **??**) and C_D is the drag coefficient. For a slender object $C_{D\perp} \approx 2C_{D\|}$. This difference in the magnitude of the parallel and perpendicular drag coefficients can result in a net propulsive force as illustrated in the figure.

   Challenge to the students: Can you think of "objects" for which $C_{D\perp}/C_{D\|} > 2$? Or examples of slender objects in which the drag corefficient in the "thin" direction is greater than the drag coefficient in the "thick" direction? (For a sphere, $C_{D\perp}/C_{D\|} = 1$.)

2. Time does not appear explicitly in Stokes equations (which are linear) and, consequently, time reversible. This reversibility is beautifully demonstrated in G. I. Taylor's movie on low Reynolds number flows which is now available online at:

   `web.mit.edu/fluids/ww.shapiro/ncfmf.html`.

   (The reversibility demonstration begins approximately 27 minutes into the film). Reversibility implies that a swimmer that undergoes a reciprocal deformation (i.e. a sequence of deformations that is symmetric when time is reversed), can never generate a net translation. This inability of reciprocal "swimmers" to swim at low Reynolds number, is commonly know as the **Scallop Theorem** (since, as in Purcell's paper, scallops are often used as the canonical example of a swimmer that can only undergo reciprocal deformations). In "Life at low Reynolds number," Purcell suggests a number of ways to beat the Scallop Theorem that are *intrinsic* to the swimmer (e.g. by introducing chirality to the swimmer or additional degrees of freedom).

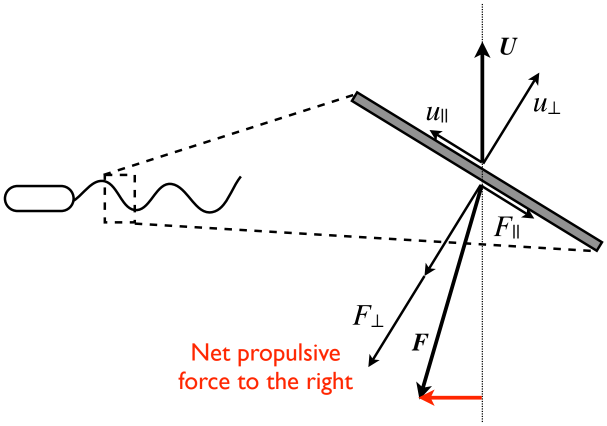


Figure 2: Net propulsive force generated by a deforming tail.

Challenge to students: (Originally posed by Purcell) A three-link swimmer consists of three rigid pieces (two "arms" and a "body") connected by hinges; time-varying torques can be independently applied at each of the hinges. Imagine that the swimmer is activated in the following sequence (start with both arms up): (1) arm 1 moves down, (2) arm 2 moves down, (3) arm 1 moves up, (4) arm 2 moves up. Which direction does this three-link swimmer go? (See "Life at low Reynolds number" for an illustration of the swimmer; see Becker, Koehler & Stone *JFM* **490** (2003) for the solution.)

However, in addition to *intrinsic* solutions, there has been a recent surge in interest in developing strategies to beat the Scallop Theorem that are *extrinsic* to the swimmer. The key idea here is to make things **soft**. For example on can:

(a) Put the swimmer near a "soft" interface (e.g. a free surface, membrane, or elastic solid). The flow around the swimmer induces deformations in the interface and the resulting change in geometry introduces a source of nonlinearity that can break symmetry.

Reference: Trouilloud, Yu, Hosoi, & Lauga "Soft swimming: exploiting deformable interfaces for low Reynolds number locomotion" *PRL* (2008).

(b) Give the surrounding fluid a "soft microstructure" which leads to a viscoelastic constitutive relationship. (Other people will talk about this at this summer school so I will not discuss swimming in viscoelastic fluids here.)

In addition to making things soft, one can also beat the Scallop Theorem by **swimming with friends**. See for example:

Reference: Lauga & Bartolo, "No many-scallop theorem: Collective locomotion of reciprocal swimmers" *PRE* (2008).

3. In optimization calculations we need to choose a metric to quantify what is being optimized. Common goals in locomotion studies include:

(a) Maximize speed for a given power ("sprinter") or
(b) Maximize efficiency for a given speed ("endurance").

Since time does not appear explicitly in the Stokes equations (which are linear), at low Reynolds numbers *speed and efficiency are equivalent measures of performance.* The efficiency is generally defined as:

$$\eta = \frac{\text{Rate of useful work}}{\text{Rate of viscous dissipation}} = \frac{\text{Force} \cdot \text{Velocity}}{\Phi} = \frac{\alpha V^2}{\Phi}.$$

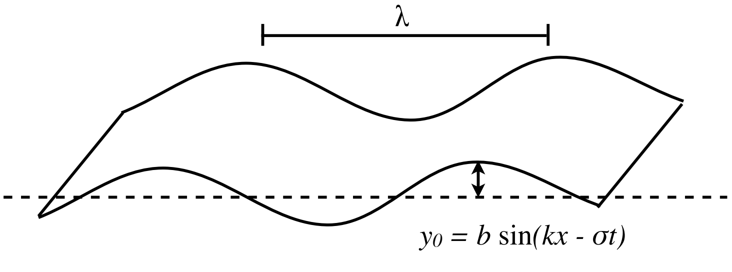
The second criterion, maximizing efficiency for a given speed, corresponds to maximizing η. Likewise, maximizing speed for a given power (fix Φ and maximize V) also corresponds to maximizing η. These two criteria, associated with speed and endurance, are equivalent at low Reynolds numbers because time can be scaled out of the equations and the performance of the stroke is determined by purely by geometric considerations. Typical efficiencies for low Reynolds number swimmers are 1-2%; I would consider 10% to be a fantastically good efficiency for a low Reynolds number swimmer. In general, if authors cite numbers that are as high as (or higher than) 10% they have used a different definition of η.

As an aside, Purcell worried about these low efficiencies (why would nature select organisms that are so inefficient?). To understand this, he calculated the power *per unit mass* for microorganisms which he found to be on the order of 0.5 W/kg which is low-ish relative to larger organisms. Purcell likened this to "driving a Datsun in Saudi Arabia": it's not a great car but it's cheap to fill up the tank.

0.3 Simple Swimmers

In the next part of the lecture we will review a simple model for a specific low Reynolds number swimmer, the 2D swimming sheet as analyzed by G. I. Taylor in 1951:

Reference: G. I. Taylor "Analysis of the swimming of microscopic organisms" *Proc. Roy. Soc. A*, **209** (1951).



For his swimmer, Taylor considered an infinite, inextensible sheet undergoing small amplitude sinusoidal deformations. The vertical displacement of the sheet is perscribed by a traveling wave $y_0 = b\sin(kx - \sigma t)$ moving with wave speed $c = \sigma/k$. Recall that the Stokes equations can be rewritten using the stream function as:

$$\nabla^4 \psi = 0 \tag{1}$$

where ψ is the stream function and is related to the velocity field, $\mathbf{u} = (u, v)$, by $u = -\frac{\partial\psi}{\partial y}$, $v = \frac{\partial\psi}{\partial x}$. This equation must be solved subject to the boundary conditions:

- No slip at the sheet: $\mathbf{u} = \mathbf{u}_{sheet}$ at $y_0 = b\sin(kx - \sigma t)$ and
- $\mathbf{u} = \mathbf{0}$ as $x \to \infty$ or $\mathbf{u} = (-V, 0)$ in a frame moving with the sheet where V is the swimming velocity.

The general solution to (**??**) is given by:

$$\frac{1}{\sigma}\psi = \sum_{nodd}^{\alpha}(A_n y + B_n)e^{-ny}\sin nz + \sum_{neven}^{\alpha}(C_n y + D_n)e^{-ny}\cos nz - \frac{Vy}{\sigma}$$

where $z \equiv kx - \sigma t$. (Note that in addition to A_n, B_n, C_n and D_n, V is also unknown and must be found by applying the boundary conditions.) Taylor then assumed $bk \ll 1$, expanded in powers of bk, and half a page of algebra later, found $V = 0$ at lowest order (i.e. no swimming). The next order correction is found many, many, many pages of algebra later (which I will not write out here) to be :

$$\frac{V}{C} = \frac{2\pi^2 b^2}{\lambda^2}(1 - \frac{19}{4}\frac{\pi^2 b^2}{\lambda^2}).$$

Thus the sheet travels $\approx \frac{\lambda}{84}$ in one cycle (which is consistent with what is observed in live microorganisms).

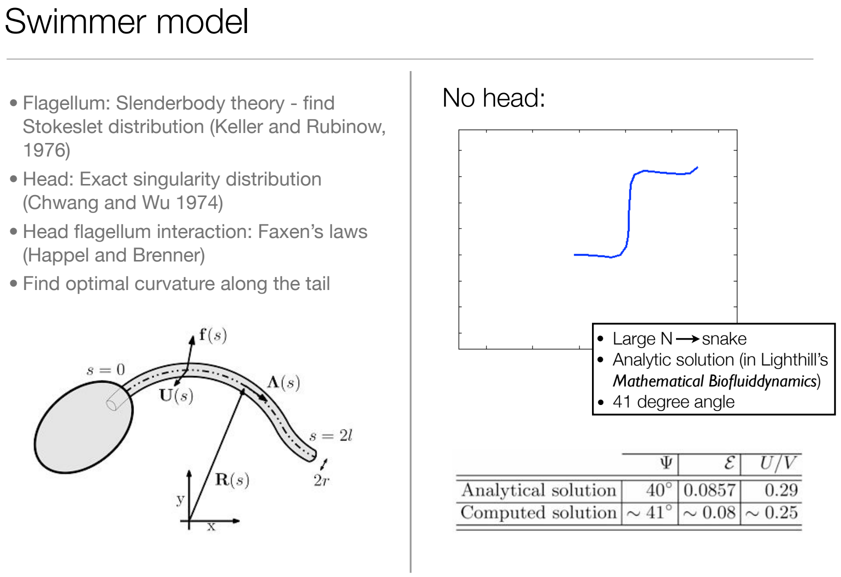
0.4 Slightly Less Simple Swimmers

In the final part of the this lecture I will discuss recent work from our group (primarily done by Daniel Tam) on slightly more realistic mircoswimmers. This part of the lecture was given in Powerpoint format and the slides have been included here as figures. We consider a swimmer that consists of a spherical head attached to a slender tail. The swimmer is allowed to select the kinematics of the tail (as is the case with eukaryotic flagella) and we seek the optimal curvature of the tail as a function of s, distance along the flagellum and t, time. The tail is modeled using slenderbody theory and the head is modeled as a singularity distribution (for details, see references on the slide shown in Figure **??**).

To test the model we first consider an organism with no head. The optimal wave form is numerically found to be a sawtooth, consistent with the analytic optimal solution found by Lighthill for an infinitely long swimming snake (see table in Figure **??** for a quantitative comparison).

Next we consider an organism with a spherical head and find that optimal strokes have several characteristics that are consistent with what is observed in nature:

- Optimal strokes contain approximately one wavelength.
- Optimal wave shapes are *not* sinusoidal rather they consist of localized regions of high curvature connected by segments of low (approximately zero) curvature.
- The optimal curvature gradually decreases from head to tail.



Swimmer model

- Flagellum: Slenderbody theory - find Stokeslet distribution (Keller and Rubinow, 1976)
- Head: Exact singularity distribution (Chwang and Wu 1974)
- Head flagellum interaction: Faxen's laws (Happel and Brenner)
- Find optimal curvature along the tail

No head:

- Large N ⟶ snake
- Analytic solution (in Lighthill's *Mathematical Biofluiddynamics*)
- 41 degree angle

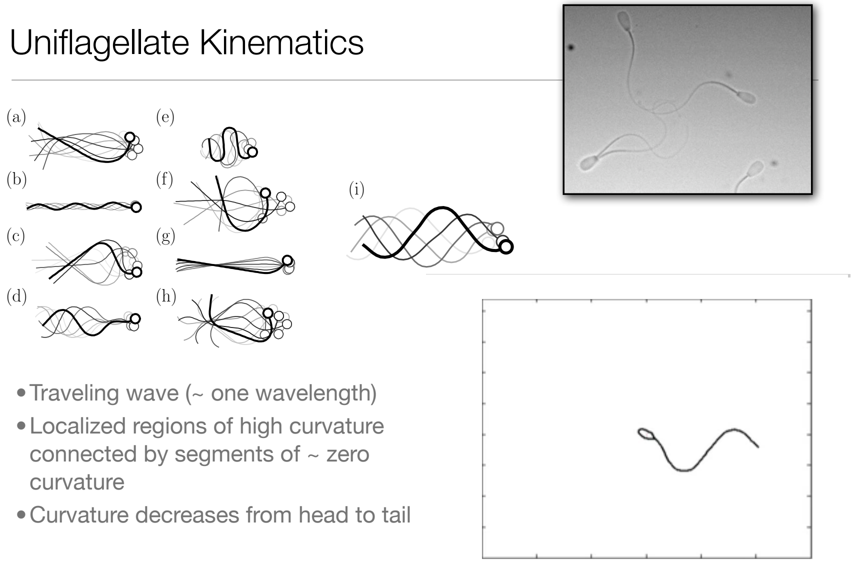
	Ψ	$\mathcal{E}$	U/V
Analytical solution	40°	0.0857	0.29
Computed solution	$\sim 41^\circ$	~ 0.08	~ 0.25

Figure 3: Single tail swimmer model.

These optimal strokes, along with sample initial guesses used in the optimization routine are shown on the slide in Figure **??**. While this qualitative comparison with live organisms is promising, it is difficult to make quantitative comparisons with biological data as finding high resolution kinematic data is challenging. However, although detailed kinematic data is lacking, there is quite a bit of data available on *morphology*.

To determine whether optimal morphologies for swimming have evolved in nature, we consider a specific microorganism with a well-defined objective function, the spermatozoon. It can be argued that spermatozoa have one primary objective: to deliver a package of genetic material to the egg. Hence we consider the following question: For a given head size (containing the genetic cargo) what is the optimal length of the tail for propulsion? One can argue that such an optimal length should exist by considering two extreme tail lengths, L. As $L \to 0$ the organism cannot move and the swimming efficiency goes to zero. As $L \to \infty$ all of the energy goes to moving the infinitely long tail rather than the precious genetic payload and again the efficiency goes to zero. Since there are tail lengths for which the efficiency is not zero (and the optimal efficiencies appear to vary smoothly with L), there must be at least one optimal value between these two extremes. Figure **??** shows computed optimal efficiencies for various values of head-to-tail length ratio. Note that every point on this curve corresponds to an optimization calculation and the optimal kinematics for short tails may not be the same as the optimal kinematics for long tails. Our computations indicate that the optimal value of $L/2R$ is ≈ 12 which corresponds with the peak in the histogram containing data from over 400 mammalian species! We can now postulate that the morphologies of spermatozoa have evolved into optimal geometries for low Reynolds number swimming.

However, one could argue that the most interesting data points in the histogram are the ones that are *far* from optimal as those points represent species are either suboptimal or have been subject to unique evolutionary pressures and constraints. In our data set, the organisms at the far right (long tailed sperm) correspond to several species of bandicoot and other mammals with



Uniflagellate Kinematics

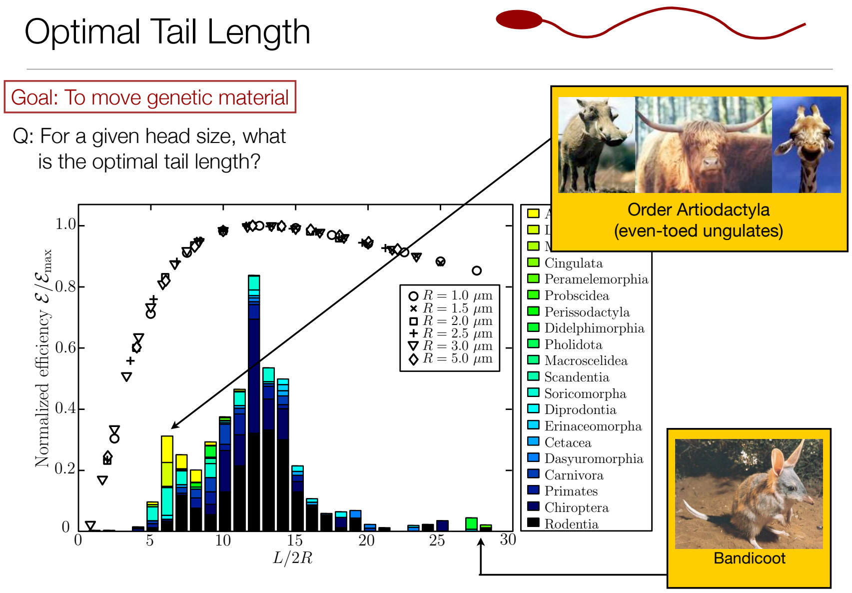
- Traveling wave (~ one wavelength)
- Localized regions of high curvature connected by segments of ~ zero curvature
- Curvature decreases from head to tail

Figure 4: Initial guesses for the optimal stroke pattern. All initial conditions converge to (i).

unusually thick tails. These organisms violate our assumption that the radius of the tail is set by the 9+2 microtubule structure discussed earlier as the flagellum is encased in a thick sheath with adds mechanical toughness. At the other end of the spectrum (short tails) the outliers correspond to monotremes, the egg-laying mammals. In these species the head of the sperm has a helical shape, far from our spherical approximation, so again it is not surprising that they fall far from the computed optimum.

The set of outliers that is more difficult to explain corresponds to the yellow peak in the histogram. These points indicate the even-toed ungulates (pigs, sheep, goats, cows ...). They deviate consistently from the optimal value of tail length by about a factor of two. We have been unable to rationalize this discrepancy and we leave it as a puzzle for the students. For further details, see:

Reference: Tam and Hosoi, *PNAS* 2011; Tam and Hosoi *PRE* 2011.



Optimal Tail Length

Goal: To move genetic material

Q: For a given head size, what is the optimal tail length?

Figure 5: Data points show optimal efficiencies as a function of head-to-tail length ratio, $L/2R$; the histogram represents the number of mammalian species that exhibit a given value of $L/2R$.